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ORIGINAL PAPER

Deep-sea video technology tracks a monoplacophoran to the end of its trail (Mollusca, Tryblidia)

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Abstract

Originally known as fossils from the Cambrian to the Devonian, the finding of a living monoplacophoran mollusc in 1952 was one of the great zoological discoveries of the twentieth century. Now, over 35 living species have been documented from deep-sea locations around the world, mainly from samples collected with trawls. Encountering these animals is extremely rare, and in situ observations are scant. Here, we report two new sightings and ecological data for a probable undescribed species of *Neopilina* including the first ever high-definition close-up video of these monoplacophorans in their natural environment, obtained while exploring seamount environments in American Samoa. Extensive trackways, similar to those associated with the monoplacophoran siting, may be evidence of a larger population at both seamounts. Living monoplacophorans are important to understanding the recent evolution of deep-sea fauna, yet their habitat, on polymetallic nodules and ferromanganese crusts, is under rapidly increasing pressure for deep-sea mineral extraction.

Keywords Molluscan evolution · Monoplacophora · trackways · ROV · Deep sea · marine conservation

Introduction

When a living monoplacophoran was recognised in 1952 (Lemche 1957), it was hailed as one of the great zoological discoveries of the twentieth century (Lindberg 2009). These molluscs had previously been found as fossils from the Cambrian to the Devonian, but living species or even more recent fossils were unknown. Monoplacophora represents a distinct taxonomic class, separate from all other molluscs. Unlike gastropods, the animals have no eyes or head per se, their body musculature is anchored to a conical shell by eight pairs of dorso-ventral muscles, and they have gills on both sides of the foot, though these features are not visible in vivo when the animal is attached to the substratum. They remain rare, specimen material is difficult to access, and little is known about their basic biology.

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Over 35 living monoplacophoran species have now been documented from deep-sea locations around the world (Ivanov and Moskalev 2007; Schwabe 2008; Haszprunar and Ruthensteiner 2013), and several species have not been formally described and named. Their rarity means that most biological observations have been taken opportunistically, although two species have been recollected from the regions of their first discoveries (Menzies et al. 1959; Lowenstam 1978; Wilson et al. 2009). As in other deep-sea molluscs, monoplacophorans are apparently reasonably tolerant to the transition to surface pressure and temperature, and species in several genera have been observed alive after recovery to the surface (Lowenstam 1978; Marshall 1998; Urgorri et al. 2005; Schrödl et al. 2006; Ivanov and Moskalev 2007; Wilson et al. 2009). Molecular sequence data have been published for seven species (Wilson et al. 2010; Kano et al. 2012; Stöger et al. 2013) including one partial and two complete mitochondrial genomes to date (Stöger et al. 2016).

Living monoplacophorans remain enigmatic in the scope of molluscan evolution (Sigwart and Lindberg 2014). Fossil and living 'Monoplacophora' are a paraphyletic, or perhaps polyphyletic, assemblage of cap-shelled organisms (Haszprunar and Ruthensteiner 2013). The clade Tryblidia more specifically conscribes species that share similar patterns of muscle attachment scars. Even so, tryblidian monoplacophoran fossils are primarily known from the Silurian and Devonian (ca. 400 million years ago), with no further fossils until the Cenozoic (Warén and Gofas 1996). Based on molecular clock estimates, living monoplacophorans share a common ancestor as recently as the Late Cretaceous, 83.2 Ma (Kano et al. 2012; Stöger et al. 2013). This gap of some 300 million years in the fossil record provides room for doubt about whether even Tryblidia is monophyletic.

The 'living fossil' monoplacophorans are more accurately a rare group of relatively recently derived and nonetheless very strange molluscs. This clarification is relevant to broader issues of understanding the evolution of deep-sea biodiversity. In contrast to the historically conventional view of a near-empty abyss populated by relic faunas, in fact, many deep-sea groups have suffered the effects of past mass extinctions and climate change (Vrijenhoek 2013; Herrera et al. 2015; Chen et al. 2017). Deep-sea ecosystems are spatially and temporally heterogeneous on similar scales as terrestrial biota (Levin et al. 2001). Likewise, deep-sea systems and the molluscs that inhabit them are susceptible to modern anthropogenic environmental disturbance (Ramirez-Llodra et al. 2011; Sigwart et al. 2017; Sweetman et al. 2017).

Technological developments are making rapid strides toward improving our understanding of deep-sea animals, and the need for deep-sea conservation measures. During February to April 2017, the US National Oceanographic and Atmospheric Administration ship NOAA Ship *Okeanos Explorer* (managed by the Office of Ocean Exploration and Research) conducted the EX1702 American Samoa Expedition: 'Suesuega o le Moana o Americka Samoa'. The aim of the expedition was to provide critical baseline information of unknown and poorly known deepwater areas in American Samoa. Here, we report a remarkable observation made during this expedition: one of the deepest ever live sightings, and ecological data, for an undescribed species of monoplacophoran, including high-definition (HD) video of the animals in their natural environment.

Materials and Method

The NOAA Ship *Okeanos Explorer* conducted high-resolution multibeam echosounder (Kongsberg EM302 30 kHz) mapping of submarine features in American Samoa waters, focusing on seamounts, and also explored the area using the remotely operated vehicle (ROV) *Deep Discoverer* and the camera platform *Seirios*. The ROV was outfitted with five HD and five standard-definition video cameras. Light was supplied by 24 LED lights (144,000 lm). Paired lasers (10 cm apart) mounted on the main high-definition video camera were used for scale. The ROV traversed the seafloor at a speed of approximately 0.1–0.3 knots. The ROV and camera platform also had a Sea Bird 9/11+ CTDs with a dissolved oxygen (DO) sensor, two hydraulic manipulators (Shilling Orion and Kraft Predator with force feedback), a sampling scoop tool, and four bioboxes.

The seamounts targeted in this study, 'Leoso' (dive 05) and 'Utu' (dive 08), are ~ 126-km apart and are situated to the south of the Manihiki Plateau (see dive data noted in Results, below). 'Leoso' and 'Utu' seamounts are located approximately 200 km north of the Samoan hotspot track, which is comprised of an age-progressive chain of volcanoes and seamounts that are anchored to the volcanically active (and biologically diverse) Vailulu'u seamount (Staudigel et al. 2006). 'Leoso' and 'Utu' seamounts are volcanic in origin, but their ages, and whether they are isolated seamounts or share a common origin with a volcanic hotspot further to the east, are unknown.

Bathymetry data were collected during this expedition onboard the *Okeanos Explorer*. Maps were made in the program QGIS. Image analyses of HD video data and stills were carried out using the software ImageJ.

Results

Dark, non-periodic, sinusoidal trails clear of sediment were observed on ferromanganese-encrusted lava flows from both seamounts; the trails contrast with the 'normal' ferromanganese substrate, which has a thin veneer of sediment representing up to 100% sediment cover. These trails were identified at similar depths (only ~ 77-m depth difference) on both seamounts: 'Leoso' (dive 05, date: February 20–21, 2017 (UTC); latitude − 12.6494; longitude − 167.2722; depth 3760 ± 7 m; temperature 1.46 ± 0.01 °C; salinity 34.695 ± 0.001; dissolved oxygen 4.97 ± 0.03 mg/L) and

'Utu' (dive 08, date: February 23–24, 2017 (UTC); latitude − 12.2740; longitude − 168.3670; depth 3837 ± 1 m; temperature 1.50 ± 0.02 °C; salinity 34.687 ± 0.009; dissolved oxygen 4.86 ± 0.04 mg/L). The trails were first identified during dive 05, but no animals were found associated with the trails. During dive 08 at 'Utu' seamount, these trails were examined, and a monoplacophoran individual was found associated with the trails. A second individual was also observed close by (~ 1 m) and was also associated with sediment-cleared trails. A prior dive (dive 06) targeting shallower portions (maximum depth of 3037 m) on 'Utu' seamount revealed no evidence of this species or of the trails. Through the use of the sampling scoop, we were able to flip a monoplacophoran individual over to ventral side up, but were unable to collect the specimen.

Video footage documented two individuals during a single dive (dive 08) at 'Utu' seamount (12.2740 S, 168.3670 W, 3837 ± 1 m; Fig. 1). Trails were observed over an area of seabed approximately 440 ± 50 m^2, and within that area, about 25–30% of the surface was covered by trackways (i.e. sediment-cleared trails) corresponding to feeding trails tentatively attributed to the monoplacophorans (Fig. 2). Feeding trails had an average width of 10 mm (s.d. 1.6 mm, $n = 30$).

The two individuals observed had shells that measured 12 ± 1 mm wide, 20 ± 1 mm long, ~ 5 mm high (Fig. 2b), and 13 ± 1 mm wide, 19 ± 1 mm long, ~ 5 mm high (Fig. 3a, b, d). The shell apex is anterior (as in all monoplacophorans), positioned within the shell margin. Dorsally, the shells were marked with numerous distinct wear scratches (Figs. 2 and 3). Based on the relatively large size and evidence of accumulated shell wear, the specimens are considered to be unequivocally adult.

Based on the single specimen seen in ventral view, these animals can be identified as genus *Neopilina*. The specimen had five pairs of long gracile gills each with at least six

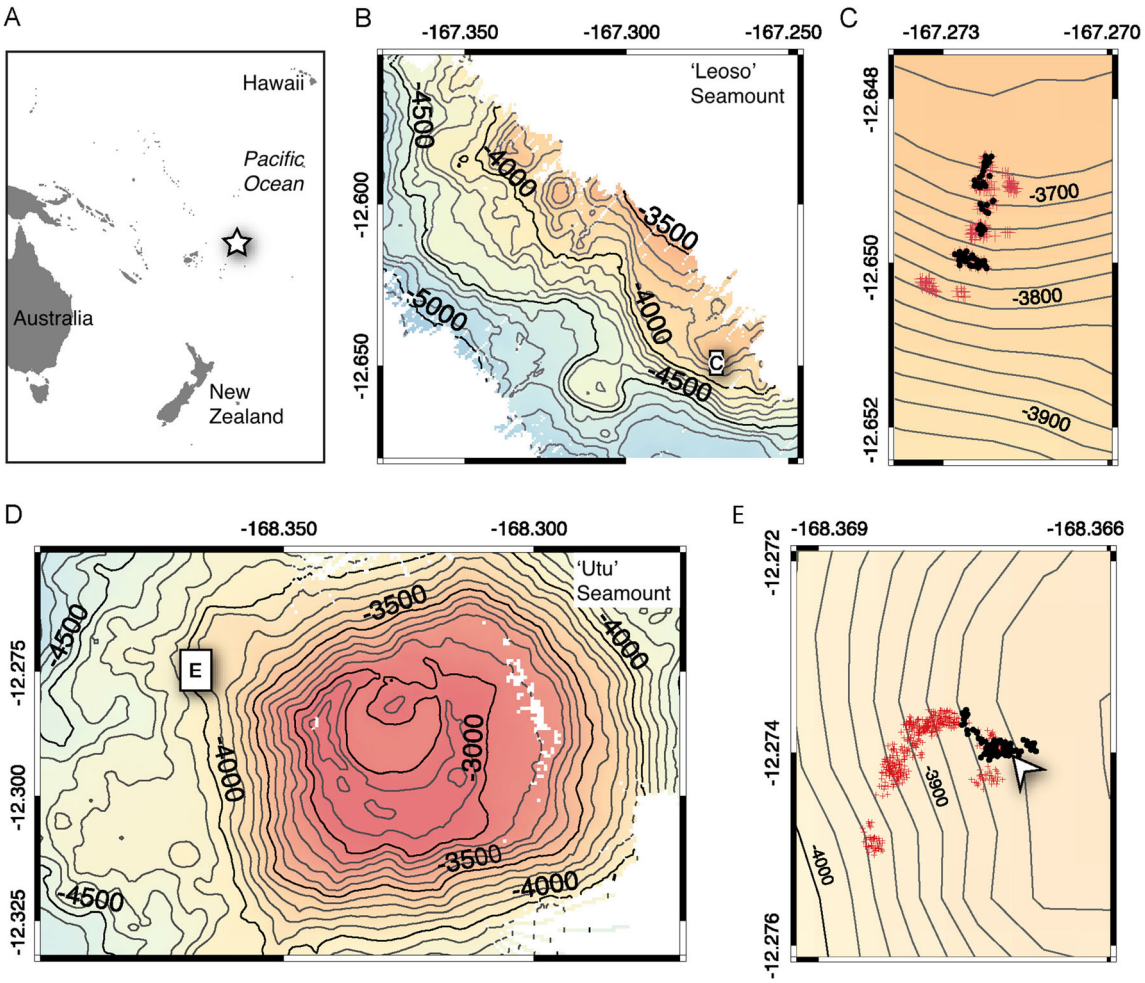

Fig. 1 Locations of study sites. **a** The star indicates the location of the study sites off American Samoa in the southwest Pacific Ocean. **b** Bathymetric map of seamount 'Leoso' with the study site indicated by a white rectangle with the letter 'C'. **c** ROV dive track and monoplacophoran observations on seamount 'Leoso'. **d** Bathymetric map of seamount 'Utu' with the study site indicated by a white rectangle with the letter 'E' (bottom, site of monoplacophoran observations). **e** ROV dive track and monoplacophoran observations on seamount 'Utu'. Black and grey lines on **b** and **d** indicate 500 and 100 m bathymetry contours, respectively. Crosses on **c** and **e** indicate ROV positions on the bottom; dots show those where monoplacophoran trackways were observed. Arrowhead indicates position of live monoplacophoran sighting (two individuals)

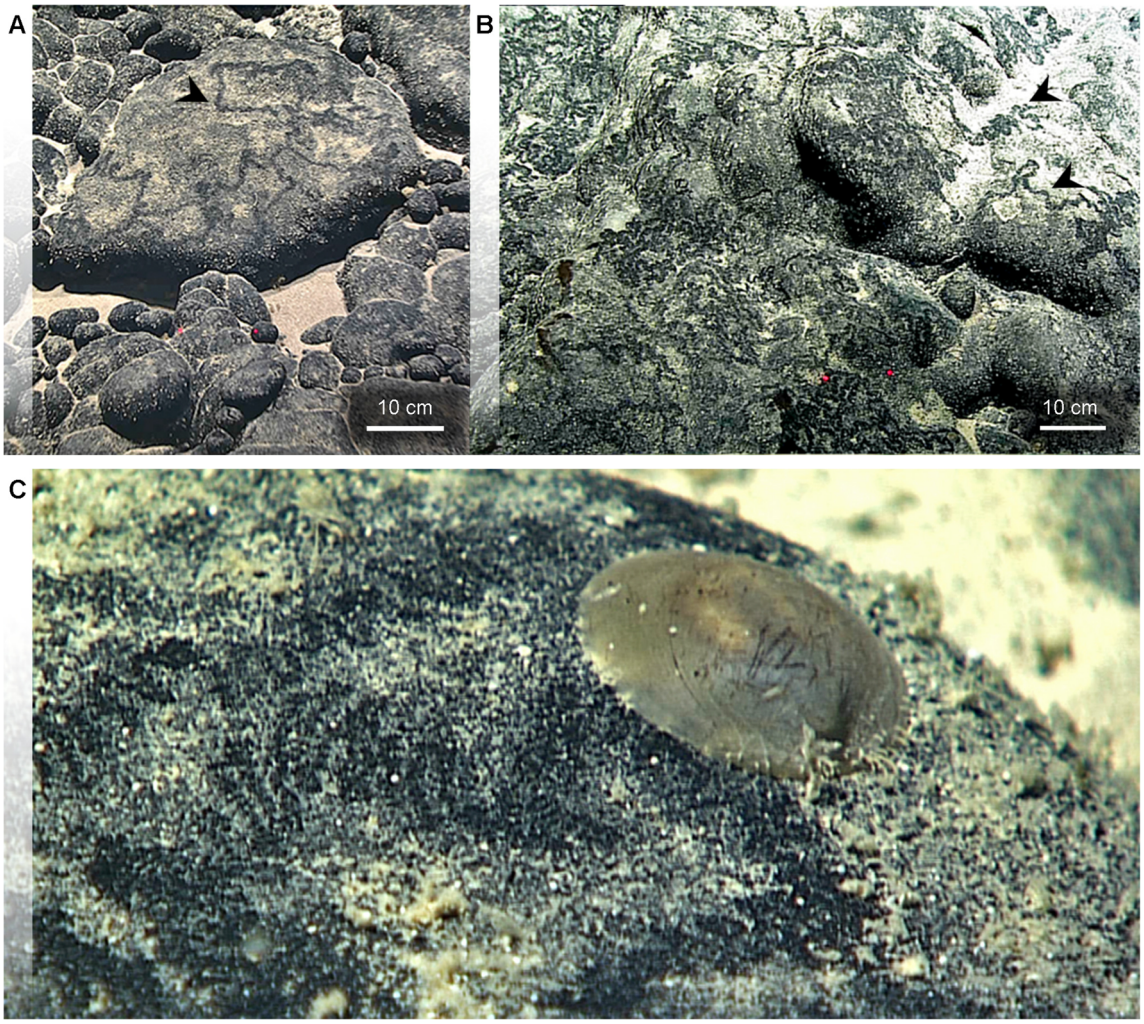

Fig. 2 Trackways attributed to *Neopilina* sp. in still images from HD video. **a** Overview of rock surface marked with feeding trails at 'Leoso' seamount (where no animals were observed). **b** Trackways at 'Utu' seamount; red dots are laser sights 10 cm apart, C. *Neopilina* sp., at 'Utu' seamount, close-up showing apparent radular scratches within trackway. Original video data from the NOAA Office of Ocean Exploration and Research (Supplementary Video)

lamellae (Fig. 3). The oral velum was broad, with the posterior aspect completely covering the postoral lappets; the mouth and velum appear continuous (i.e. right and left vela appear to be joined anteriorly to the oral hood; Fig. 3b).

These monoplacophorans have shell morphology and body size and occur at depths that are similar to *Neopilina galathaea*; however, the gills of these new specimens are long and gracile (Fig. 3), different from the broad lamellae described in the detailed anatomical account (Lemche and Wingstrand 1957) and seen in other specimens (Scripps Institution of Oceanography Benthic Invertebrate Collection, SIO-BIC M913) of that species. No other monoplacophorans have previously been reported from the Western South Pacific (the other closest known records are from, e.g. the Hawaiian Islands, over 4000 km away) and the animals are therefore inferred to belong to an undescribed species.

The animals appear to have been grazing directly on the soft sediment covering the hard ferromanganese substratum. A faecal pellet, visible in ventral view, is the same colour and texture as surrounding detritus (pale material at the anus in Fig. 3a). Some sediment near the animals also had a pelleted texture which could be compared to shed faecal matter. Finer marks on trackways (approximately 1/10 of the width of the trails) where the sediment has been displaced correspond to the general appearance of other molluscan radula scratchings (Fig. 2). The coincidence of animals and trackways points to a conclusion that these monoplacophorans are moving across hard substratum, grazing on the overlying detritus.

Discussion

Several species of monoplacophorans have been observed and photographed alive, usually when they were collected attached to a polymetallic nodule or other object (Urgorri et al. 2005; Wilson et al. 2009; Wiklund et al. 2017). The *Neopilina*

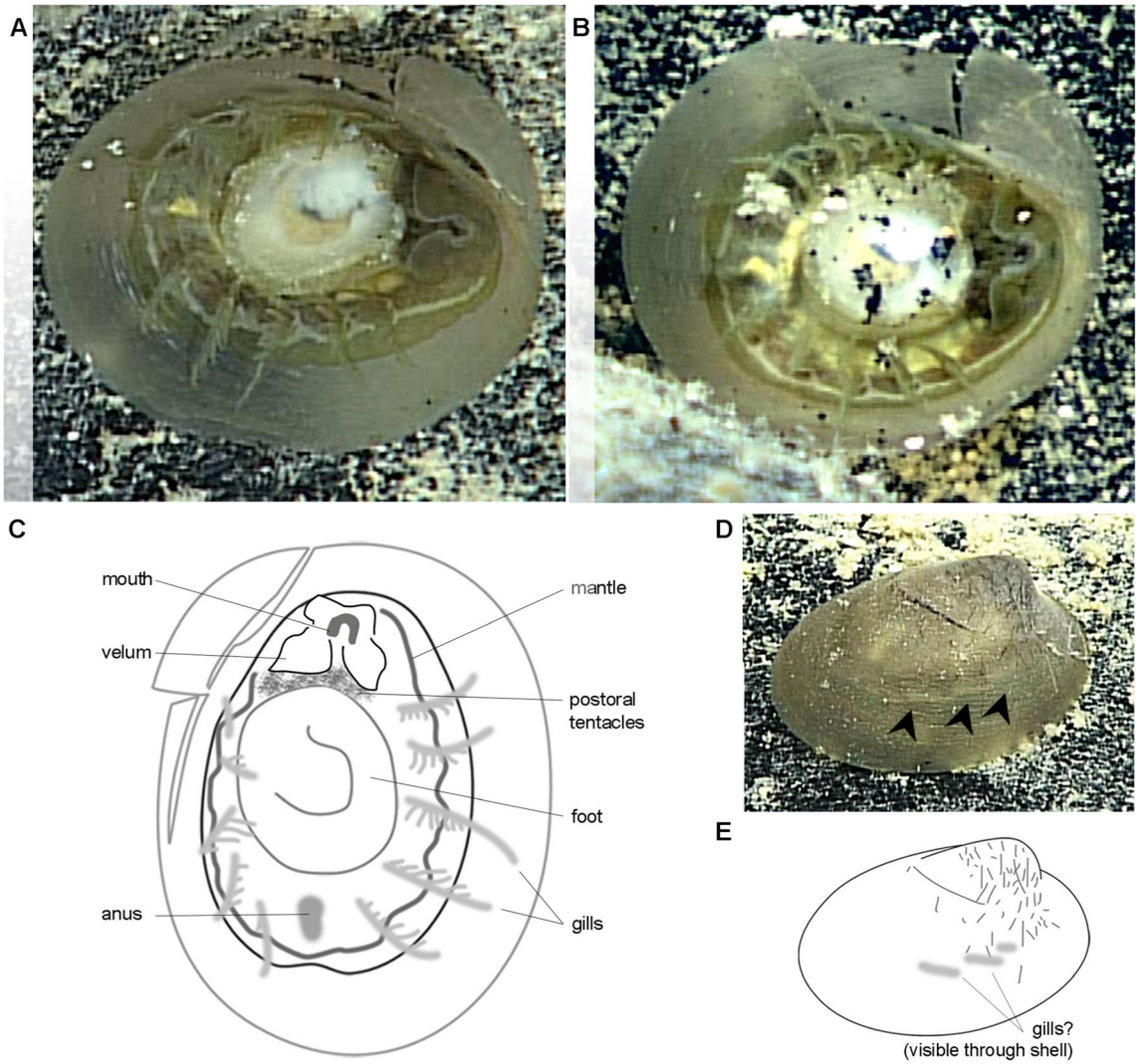

Fig. 3 *Neopilina* sp., still images from HD video to show morphological features. All images in this figure are of the same individual. **a**, **b** Ventral view. **c** Line drawing of ventral view indicating key features. **d** Lateral view of dorsal shell. **e** Line drawing of shell. Anterior is to the right in all parts except **c** (anterior at top). Original video data from the NOAA Office of Ocean Exploration and Research (Supplementary Video)

sp. in American Samoa were found attached to continuous bedrock, so would never have been collected by conventional grab sampling, and confounded the effort in this study to collect one via the ROV. The present new record expands the diversity of living monoplacophorans, but fits within the known geographical range, bathymetry, and body size for the group. This contribution adds a record of the animals in situ, and observations of the soft parts without the effects of pressure and temperature changes associated with collecting the specimens to the sea surface. The trackways indicate a potentially much larger local population.

Comparisons with other living monoplacophorans

Living monoplacophoran species are mostly small, at most 3 mm in shell length. Prior to this record, there were only six species that exceeded 10 mm. Across global monoplacophoran diversity, small species (up to about 5 mm), include a broad bathymetric range, from 180 m to over 6300 m deep; the Antarctic species *Laevipilina antarctica* has a broad eurybathic distribution from 210 to 3136 m (Schrödl et al. 2006). The largest species (over 10 mm) are restricted to abyssal depths, and all are from depths of 3000–6489 m (Haszprunar 2008). This new record for *Neopilina* (3760 to 3837 m) thus falls within the expected depth range for a large-bodied monoplacophoran.

The larger species of monoplacophorans are in three genera: *Adenopilina* (a single species from the Gulf of Aden, Arabian Sea), *Vema*, and *Neopilina*. The present record differs from *Vema* spp., which are from even deeper waters and have six pairs of gills rather than five. New gills are added anteriorly during ontogeny (Warén and Hain 1992), and the individual gills add new lamellae (Moskalev et al. 1983). Adult gill count appears to be fixed and has been used to differentiate these two genera (Warén and Gofas 1996).

Features of the body as well as the shell have been described for most living monoplacophorans (Ivanov and Moskalev 2007). It is not entirely clear what level of distortion is caused by processes of collection and preservation. Comparison is limited from the present video footage because of the restricted viewing angles and magnification. For example, the postoral tentacles were mostly obscured by the velum here, and similarly, *Laevipilina cachuchensis* had flexible velar lobes and gills that were more extended when alive than after preservation (Urgorri et al. 2005). The comprehensive descriptions of *N. galathaea* mentioned concern about preservational distortion of the gills, and those authors restricted their gill observations to a specimen where shell breakage protected the gill lamellae from compaction by sediment (Lemche and Wingstrand 1957). The unusually long and gracile gills on this new *Neopilina* sp. are strikingly different even from other species that have been figured from live photographs (e.g. Urgorri et al. 2005), but all previous observations of soft parts were at the surface after collection. Although long and clearly visible, the gills of this *Neopilina* sp. did not move during the available video. This is in contrast to a vibrating motion reported from aquarium observations of *Laevipilina hyalina* (Lowenstam 1978). Those historical experiments likely caused unusual stress to the animals, including overheating by incandescent lighting, and the same movement was not reported in later aquarium observations of the same species (Wilson et al. 2009). At cold temperatures of the deep seafloor (monoplacophorans observed in American Samoa living in 1.5 °C water), ectothermic animals are expected to move slowly.

Tracking monoplacophorans

The first underwater photograph of a living monoplacophoran, and still the deepest live observation, was an image of a trail and associated shell (Menzies et al. 1959). Those authors described deep, straight, furrow-like tracks attributed to monoplacophorans, photographed at 5821-m depth. When the animal is attached to the substratum, a monoplacophoran is very difficult to distinguish from a gastropod limpet. Interestingly, there is one substantial behavioural difference that evidentially separates monoplacophorans from at least patellacean limpets. Patellogastropod limpets will not traverse even a fine layer of soft sediment or sand and will only move across a bare hard bottom (Lindberg and Pearse 1990; D.R. Lindberg, pers. comm.; the authors, unpub. obs.). This may or may not extend to other limpet-like gastropods, but the *Neopilina* sp. were traversing a silt layer overlying a hard bottom, where a patellacean limpet would not crawl, and other monoplacophoran species move freely in soft sediment. This point may be helpful in differentiating monoplacophorans in video data.

It is not clear whether all trackways observed in our study site ('Utu' seamount), including at a second nearby seamount ('Leoso'), can be attributed solely to monoplacophorans. The track dimensions are comparable to the shell width of the two adult individuals we observed, and no other animals were seen that could also have contributed such trails. Additionally, two monoplacophorans were observed in association with the trails on 'Utu' seamount, strengthening the proposed link between the trackways and the animals. The only previous trackway attributed to a living monoplacophoran, *Vema ewingi*, was comparatively very straight and did not meander as in the trackways observed here, but the observation of *Vema ewingi* was on soft substratum and the still image was constrained to a very small range of view (Menzies et al. 1959). Here, a large area was covered in criss-crossing tracks and it was not possible to attribute a single animal to a single trackway. There may have been more monoplacophorans present, as the topology was complex and included many depressions that would obscure an animal of this size (Supplementary Video).

The putative scratch marks we observed within the cleared area of a trackway very close to one specimen have the appearance of radular scraping (Fig. 2). Monoplacophoran radulae are similar to those of chitons (Haszprunar and Ruthensteiner 2013). A previous record of potential monoplacophoran radular scratches had a different appearance, but a direct comparison may be inappropriate, as those marks were on the tissue of a xenophyophore (Tendal 1985). Several descriptions have documented the gut contents of monoplacophorans, and some species may target particular food items (Tendal 1985; Warén and Hain 1992); however, as a group, they are apparently mainly detritivores that ingest sediment (Lemche and Wingstrand 1957). At least one other species, *Vema ewingi* was observed with a faecal pellet that matched the surrounding sediment (Menzies et al. 1959), as we observed apparent faecal material of *Neopilina* sp. here with the same texture and colour as the surrounding detritus.

Monoplacophoran habitats under threat

Other species of monoplacophorans retrieved from similar abyssal depths were all associated with soft sediment or where there was no sediment description the habitat was assumed to be similar to that photographed for *Vema ewingi* (Menzies et al. 1959; McLean 1979). One other species was reported from ferromanganese crust at 2000 m, similar conditions to the new record here (Moskalev et al. 1983). Yet habitat is variable even at genus level; *Neopilina* spp. are found on clay (*N. galathaea*), on silt on hard bottom or boulder (*N. rebainsi*, and herein), and on gorgonian coral (*N. starabogatovi*). Monoplacophorans as a whole are found on soft sediment, hard bottoms, nodules, and biotic substrata (Ivanov and Moskalev 2007). Six species in four genera have been found living on polymetallic nodules, including the most accessible living monoplacophoran *Laevipilina hyalina* (Urgorri et al. 2005; Ivanov and Moskalev 2007; Wilson et al. 2009). These new records of *Neopilina* sp. were found on a ferromanganese-encrusted seamount. Although monoplacophorans are perceived as rare, there are hundreds of seamounts spanning similar depths

(Staudigel and Koppers 2015) in the South Pacific region, which may represent suitable habitat for these molluscs.

Polymetallic crusts and nodules are of increasing interest as a target of the rapidly developing field of deep-sea mining. Monoplacophorans, a rare and enigmatic group of organisms that live at low densities and still hold the answers to some of the great evolutionary mysteries, may be at risk from future commercial exploitation of seabed mineral resources. We still know very little about the biology of many deep-sea animals. Key biological questions can only be answered with access to physical specimens; however, in situ video observations are a proven tool to rapidly gain additional data and the environmental context for many elusive species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

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